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OPINION **Open Access**

From the scala naturae to the symbiogenetic and dynamic tree of life

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Abstract

All living beings on Earth, from bacteria to humans, are connected through descent from common ancestors and represent the summation of their corresponding, ca. 3500 million year long evolutionary history. However, the evolution of phenotypic features is not predictable, and biologists no longer use terms such as "primitive" or "perfect organisms". Despite these insights, the Bible-based concept of the so-called "ladder of life" or *Scala Naturae*, i.e., the idea that all living beings can be viewed as representing various degrees of "perfection", with humans at the very top of this biological hierarchy, was popular among naturalists until ca. 1850 (Charles Bonnet, Jean Lamarck and others). Charles Darwin is usually credited with the establishment of a branched evolutionary "Tree of Life". This insight of 1859 was based on his now firmly corroborated proposals of common ancestry and natural selection. In this article I argue that Darwin was still influenced by "ladder thinking", a theological view that prevailed throughout the 19th century and is also part of Ernst Haeckel's famous Oak tree (of Life) of 1866, which is, like Darwin's scheme, static. In 1910, Constantin Mereschkowsky proposed an alternative, "anti-selectionist" concept of biological evolution, which became known as the symbiogenesis-theory. According to the symbiogenesis-scenario, eukaryotic cells evolved on a static Earth from archaic prokaryotes via the fusion and subsequent cooperation of certain microbes. In 1929, Alfred Wegener published his theory of continental drift, which was later corroborated, modified and extended. The resulting theory of plate tectonics is now the principal organizing concept of geology. Over millions of years, plate tectonics and hence the "dynamic Earth" has caused destructive volcanic eruptions and earthquakes. At the same time, it created mountain ranges, deep oceans, novel freshwater habitats, and deserts. As a result, these geologic processes destroyed numerous populations of organisms, and produced the environmental conditions for new species of animals, plants and microbes to adapt and evolve. In this article I propose a tree-like "symbiogenesis, natural selection, and dynamic Earth (synade)-model" of macroevolution that is based on these novel facts and data.

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Background

In his *Autobiography* [1], Charles Darwin (1809 - 1882) presented a self-critical review of his achievements as a naturalist that revealed much about the character of this key figure of the evolutionary sciences and other branches of biology and geology [2-4]. With respect to the most influential of Darwin's 16 scientific books, *On the Origin of Species*, the author remarked that "Sixteen thousand copies have now (1876) been sold in England and considering how stiff a book it is, this is a large sale" [1]. This judgement is in part due to the fact that the *Origin of Species* was not designed by Darwin as a separate book; rather, it was published as an *Abstract*, taken from a much larger manuscript entitled *Natural Selection* [5]. Ironically, Darwin's major, scheduled "Magnum opus" with the tentative title *Natural Selection* never appeared in print, but the *Extract* published by the author in November 1859 in order to establish priority with respect to his theory of the "preservation of favourable variations and the rejection of injurious variations" became a best- and longseller [6].

The second and more important reason for the "stiffness" of Darwin's *Origin of Species* is attributable to the almost complete lack of illustrations. In contrast to Darwin's books on botanical and zoological issues, which contain numerous pictures [2-4], his *Abstract* published

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in 1859 (6th and final edition, 1872) [6,7] contained only one rather "sterile" diagram, a phylogenetic scheme. This "tree-like" figure is part of Chapter IV entitled "Natural Selection" in the first edition [6], and re-named "Natural Selection; or the Survival of the Fittest" in the 6th and final version of the "Species book" [7]. It should be noted that the phrase "survival of the fittest" was borrowed by Darwin from the philosopher Herbert Spencer (1820-1903), who was also the first to introduce the word "evolution" *sensu* phylogenetic development (a term not used by Darwin in the first edition [6]) into the emerging biological sciences of the 19th century [5].

With reference to his abstract illustration, Darwin explained at length the principle of "descent with modification by means of natural selection", and concluded, with his Bible-educated readers in mind, that "On the view that each species has been independently created, I can see no explanation of this great fact (i.e., the relatedness of all animals and all plants) in the classification of all organic beings; but, ..., it is explained though inheritance and the complex action of natural selection, entailing extinction and divergence of character as we have seen illustrated in the diagram" [6] p. 100.

Although Darwin made many changes and added entire sections to the text during the five revisions of his original version of the *Origin* [6], one key sentence remained unchanged: At the end of Chapter IV, the author wrote, with reference to his tree-like diagram, that "As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications" [6], p. 101; [7], p. 137.

In this article I argue that the metaphorical "Tree of Life"-statement quoted above was still heavily rooted in the religious pre-Darwinian "evolutionary ladder-" or *Scala Naturae*-thinking of earlier naturalists. In the second part of this account I show that Darwin's view of a static, "Animals and Plants-based Tree of Life" that does not take into account micro-organisms and endosymbiotic events, is outdated. Finally, I review evidence indicating that the dynamic Earth (plate tectonics), geological processes unknown to Darwin, must be integrated into a more realistic picture of the evolution of life on our ever changing "planet of the microbes" [5].

From the earliest Moral Tree to the Great Chain of Being

The Spanish philosopher and theologian Ramon Llull (1232-1315) was one of the first to publish a tree-like scheme illustrating the growth and interrelationships of the basic knowledge of his time. Born into a wealthy family in Palma, and well educated, he worked as a teacher in Majorca and Paris. Llull's diagram of the "apostolic and moral tree" (Figure 1) formed part of a unified system of knowledge. At the top of this extensively rooted tree, Jesus, the incarnation of the Biblical God, is depicted, surrounded by the latin words "gloria" (fame) and "pena" (penalty). The woodcut depicted here is a modified version of the original that does not show all the details [8]. In his writings, Ramon Llull argued that there is no difference between philosophy (i.e., natural history) and Bible-based theology, and therefore between reason and faith [8,9]. Hence, even the most absurd mysteries may be proven by means of logical inferences and the use of Llull's *Ars Magna* [9]. This way of thinking removed all distinctions between natural (fact-based) truths and supernatural (spiritual) myths.

This "rationalistic mysticism" was taken up by the followers of the Spanish theo-philosopher ("Llullists") and later evolved into an ideology that was called "Llullism" [9]. The basic tenet of the "Illuminated Doctor" is illustrated in his apostolic tree, which depicts real things (humans and a tree-like plant), mixed up with a supernatural being (Jesus, the son of God, as the crown of the "tree of knowledge") [8]. Since Llull also wrote treatises on medieval natural history (alchemy, botany), and had a great influence on the mathematician Gottfried W. Leibnitz (1646-1716), he is also recognized as a pioneer in computation theory. However, since he had several religious visions, and was a convinced Christian, Raymon Llull, throughout his later life, mixed up facts of nature and religious imaginations [9].

Although the influence of the "Llullists" may have been limited, the pre-Christian idea of the *Scala Naturae* ("Great Chain of Being") [10-14] is unequivocally related to the Bible-based scheme depicted in Figure 1. The order of the static world, between "earth and heaven", was shown and thought of as a linear sequence of bodies (from minerals via plants, animals to man). On top of this hierarchical arrangement of "created beings" we find the almighty Biblical God, who, according to Llull, had the following positive attributes: "goodness, greatness, power, eternity, wisdom, will, virtue, truth, and glory" [9].

One popular version of the *Scala Naturae*, which was published in 1779 by the Swiss naturalist Charles Bonnet (1720-1793), is shown in Figure 2. At the base of this version of the "Great Chain of Being" are non-living objects such as minerals and earth, followed by plants, insects, reptiles (snakes) and mammals. On top of this "natural ladder" we find the "Orang-Outang", followed by "L'Homme" (man) [15]. It should be noted that Bonnet, who discovered the phenomenon of parthenogenesis in insects, was convinced that species do not change over

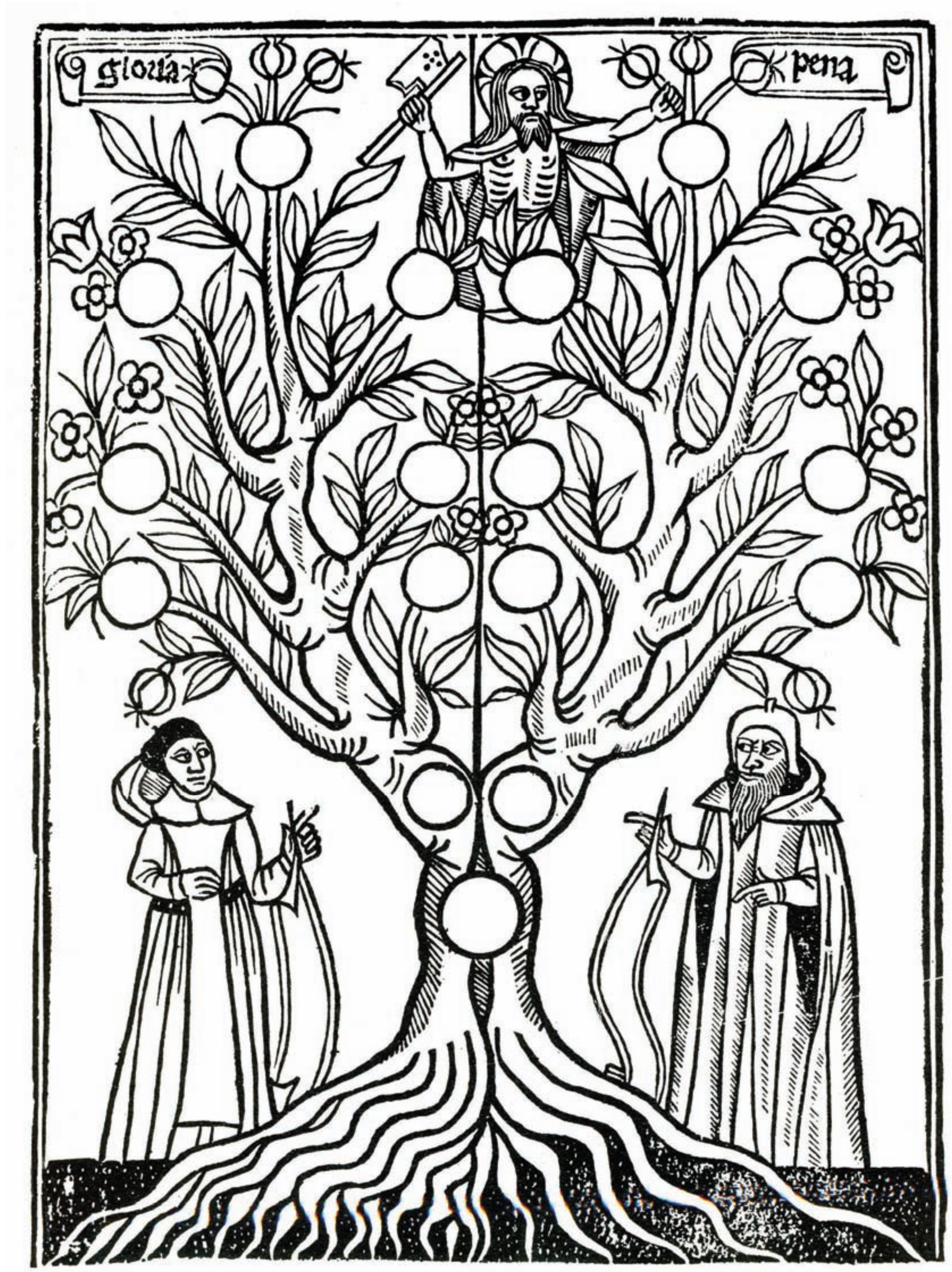

Figure 1 The "Moral Tree", published posthumously in 1505 in a book authored by Raymon Llull (1232-1315). This Spanish philosopher and Christian theologian mixed up natural phenomena with supernatural religious dogma and hence became the spiritual father of a medieval ideology called "Llullism" [part of a woodcut, adapted from ref. 8].

long time periods. In his monograph of 1779 from which the *Scala Naturae* is reproduced [15], Bonnet concluded that there is no visible change in nature, everything remains largely identical, and species are constant. Hence, Bonnet and most naturalists of his time were convinced that animals and plants are static essences created individually by the Biblical God, a religious view that Darwin attacked and thoroughly refuted [5-7,11-14].

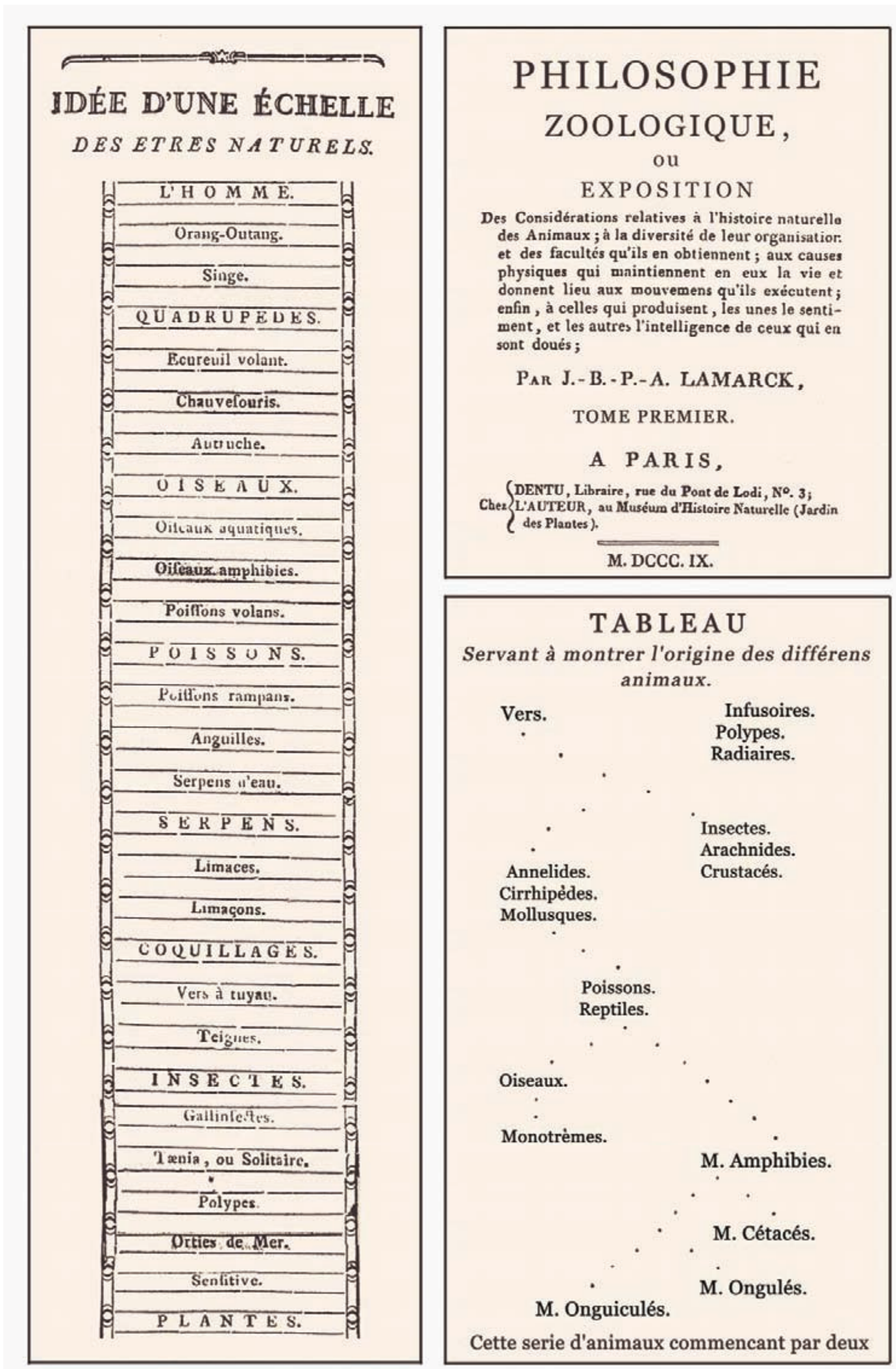

Figure 2 Upper part of the "Great Chain of Being" or *Scala Naturae*, as published in 1745 by Charles Bonnet (1720-1793) (left column). On the right side, the title page of the most influential book of Jean Lamarck (1744-1829) and his tree-like scheme of 1809 is shown [adapted from refs. 15 and 16].

Jean Lamarck and the origin of evolutionary tree-thinking

The French botanist and zoologist Jean-Baptiste de Lamarck (1744-1829) was expected by his father to take a career in the Catholic church. However, the young naturalist was not inclined to the ministry, and after his father's death in 1760 Lamarck quit his Jesuit college to become a botanist. Later, he made the switch to zoology, coined key-terms such as "invertebrates", and published new concepts on the relationships between different groups of animals [16,17].

In his most important book entitled *Philosophie Zoologique* [16], Lamarck juxtaposed the "conventional view", i.e., the dogma of independent creations of animals (and plants) as described in the Bible, with his "new opinion": According to Lamarck [16], there are ongoing spontaneous generations of primitive forms of life on Earth. Later, these non-specialized living beings transformed into "higher" animals during the history of our planet. Hence, fifty years before Darwin's *Origin of Species* was published [6], Lamarck proposed, in 1809, the principle of the gradual transformation of species and depicted his "theory of evolution" in a famous tree-like diagram that is reproduced in Figure 2.

However, a comparison of Lamarck's original scheme with Bonnet's *Scala Naturae* reveals striking similarities: The "Tableau" of Lamarck, who was an adherent of the philosophy behind the "Great Chain of Being" [14], is more "ladder-like" than a true tree with branches and twigs (Figure 2). In a subsequent book published in 1815, Lamarck depicted an "Order presuming the formation of animals in two separate series" [17]. This scheme [reproduced in ref. 14] is again more a ladder than a tree. The author distinguished between three hierarchy levels: Apathic-, sensible- and intelligent animals, respectively.

Concerning the means by which the structure of an organism altered over generations, Lamarck proposed his famous theory that is still known today as the "inheritance of acquired characteristics". According to the French scientist, changes occurred because an animal passed on to its offspring physiological changes, such as strengthened muscules it had acquired in its own lifetime, and those modifications came about in response to its survival needs. Conversely, the disuse of an organ would cause it to wither and disappear, which "explained", how snakes lost their legs etc. It should be noted that Lamarck's concept of inheritance, which is not supported by empirical evidence [18], was accepted by Darwin. In addition, Lamarck suggested that species transformations happen according to a pre-determined plan and that the results have already been decided by forces he was unable to identify.

Although Lamarck's theory of the gradual transmutation of species over long (geological) time periods was popular until his death in 1829, his ideas encountered fierce religious and political opposition, notably by Georges Cuvier (1769-1832). As a result, the achievements of Lamarck were soon forgotten so that his "principle of the gradual transformation of species" was superseded again by Biblical myths.

Charles Darwin's Tree of Life and the sterile, static hierarchy of nature

In a little-known paper of 1855 entitled "On the law which has regulated the introduction of new species" [19], Alfred Russel Wallace (1823-1913), the co-discoverer of the Darwinian "principle of natural selection" [20], described a "Tree of Life-concept" referring to "branching of the lines of affinity, as intricate as the twigs of a gnarled oak ... and to ..... minute twigs and scattered leaves". In an article published one year later, Wallace described a method of tree-building, which has recently been discussed in this journal [14].

Charles Darwin's famous first "Tree of Life"-sketch, which was supplemented by the phrase "I think" (Figure 3A), was drawn into his "Notebook B" of 1837, only one year after the junior scientist had returned from his five-year long voyage on *HMS Beagle* [5]. Darwin's sketch appears on page 36 of his "Notebook B" - the first 35 pages are taken up by considerations on the "evolutionary thoughts" of his famous grandfather Erasmus Darwin (1731-1802). The older Darwin published his revolutionary thoughts on the transformation of species in his book entitled *Zoonomia* (1794). With respect to (endothermic) mammals Erasmus Darwin wrote that "... would it be too bold to imagine that, in the great length of time since the earth began to exist, perhaps millions of years ... that all warm-blooded animals have arisen from one living filament, which the great First Cause endued with animality, ... and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity, world without end? ... as the earth and ocean were probably peopled with vegetable productions long before the existence of animals ... shall we conjecture that one and the same kind of living filament is and has been the cause of all organic life?" [21].

It has been argued that, with respect to Charles Darwin's botanical works, the influence of his grandfather may have been larger than he later admitted [3]. The passage cited above suggests that the younger Darwin developed his famous "I think-sketch" of 1837 (Figure 3 A), at least in part, under the spiritual leadership of his grandfather Erasmus.

However, what is certain is that for Charles Darwin the "Tree of Life" was not so much thought of as a

Figure 3 Charles Darwin's early sketch of an evolutionary tree (or a coral), drawn in 1837 (A). Marine organism (*Bossea arbignyana*) collected by Darwin and classified by him as a coral ("family Corallinae"). Later it was discovered that this "coral-like" inhabitant of sea waters (B) is a red alga (family Corallinaceae, Phylum Rhodophyta). Red coral (*Corallium rubrum*), which grows on rocky sea bottom either in the depths or in dark caverns (C). This wide-spread species, which is found mainly in the Mediterranean Sea, was known to Darwin and possibly served as a model for his diagram (see Figure 4) [adapted from ref. 22].

woody plant, but rather as a coral. As Bredekamp [22] has documented in detail, Darwin wrote in his "Notebook B" of 1837 that "The tree of life should perhaps be called the coral of life". This view of the "unity of life on Earth" was in part based on Darwin's hands-on experience as a geologist, who had studied coral reefs in nature. A coral-like organism, later identified as an red alga (*Bossea arbignyana*), was collected and preserved by Darwin (Figure 3 B). This living being resembles the wide-spread stone coral (*Corallium rubrum*) (Figure 3 C), which served as the living model organism for Darwin's novel concept that has been summarized under the term "tree-thinking" [23-25].

The only diagram Darwin included into the "sterile" text of his *Origin of Species* illustrates the essence of the "one long argument" developed by the author [6,7]. However, a comparison between the first and last (definitive) editions of 1859 and 1872, respectively, reveals a striking improvement of the text: Darwin (1872) had added a headline entitled "The probable effects of the action of natural selection through divergence of character and extinction, on the descendants of a common ancestor" to the text so that his discussion of the tree-like diagram became a separate paragraph in Chapter IV. On these pages of the *Origin*, Darwin's five "species theories" that were identified and described for the first time by Ernst Mayr (1904-2005) [11,12], are apparent (Figure 4):

1. Descent with modification (Darwin's definition of evolution) as a fact of nature *versus* supernatural acts of independent species creations, labelled by the author as religious dogma. 2. The principle of the last common ancestor of all forms of life (see A in Figure 4). 3. The theory of gradual, step-by-step species transformations. 4. The multiplication of species over evolutionary time (thousands of generations) and 5. The principles of natural (and sexual) selection as the major "driving forces" for the transformation of species.

In addition to these five "Darwinian species theories" [for details, see refs. 5, 11, 12], the author discussed the phenomenon of extinction. According to Darwin, the "improved descendant" of any species has the tendency to supplant and finally exterminate at each stage of evolutionary development "their predecessors and original progenitor" [6,7]. Finally, it should be noted that Darwin [6,7] unequivocally proposed a continuum between "speciation" and the evolutionary development of novel body plans, processes that were later called "micro- and macroevolution", respectively [11,12]. This concept was described by the British naturalist, with reference to his famous scheme (Figure 4), in the following words: "In the diagram, each horizontal line has hitherto been supposed to represent a thousand generations; but each may represent a million or more generations ... I see no reason to limit the process of modification ... to the formation of genera alone ... new families, or orders, are descended from two species of the original genus" [7].

Despite these tremendous insights provided by Darwin, who was one of the first to replace the "Ladder of Life" (Figure 2) by a "Tree-like concept" [22-25], our modern view of the biosphere, and the processes that have brought about the diversity of life as we know it

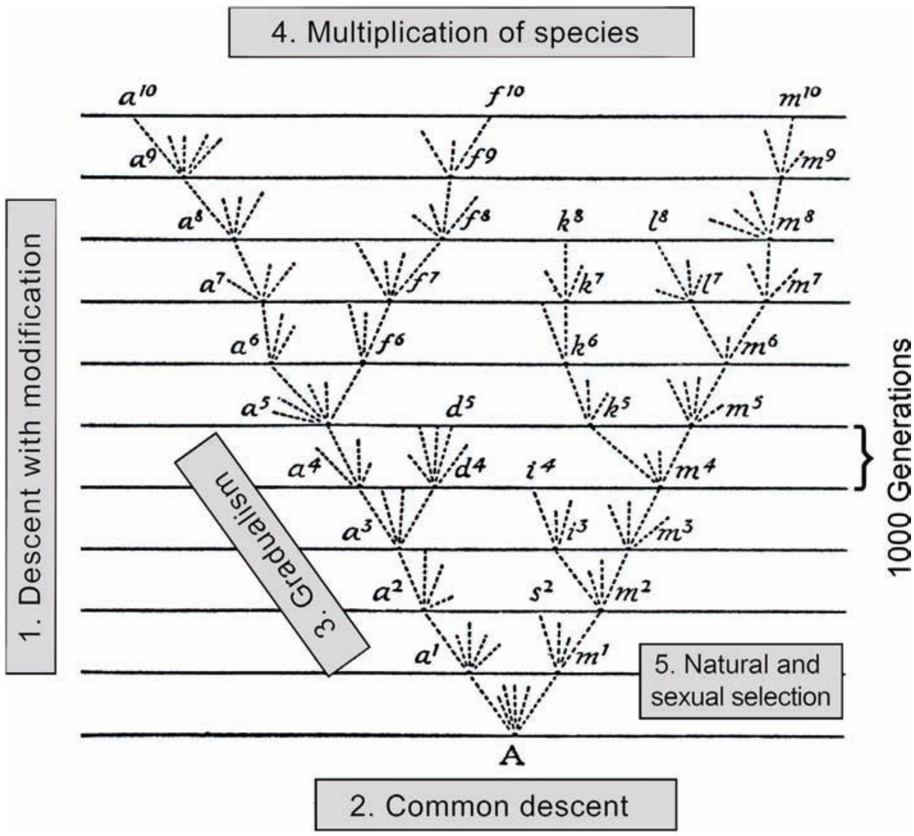

Figure 4 Partial reproduction of the single illustration in Darwin's *Origin of Species* of 1859 (6. ed. 1872). This famous diagram may have been inspired by corals (or coral-like organisms) as depicted in Figure 3 B, C. Darwin's five theories are added to the figure (1. to 5.), which illustrate the transformation and diversification of species, which originate from a common ancestor (A) [adapted from ref. 7].

today, have advanced to such an extent that Lamarck and Darwin would hardly understand our current evolutionary concepts. What are the problems with Darwin's 19th century-ideas about the evolution of life?

First, Darwin [6,7] used old-fashioned terms such as "perfection, improvement, higher vs. lower (or primitive) forms of life" etc. that are no longer in use today and may document relicts of religiously motivated "ladder-thinking" in his texts. Second, Darwin discussed in none of his 16 books in any detail the bacteria, although microbes were already known at that time [2]. In other words, the scientific work of the British naturalist is restricted to macro-organisms (animals, plants) to the exclusion of microbes. His references to "Infusoria", "Animalcules", or "Lower Organisms" [6,7] are confusing and unclear. Finally, although Darwin experienced a severe earthquake during his voyage with the *HMS Beagle* [5], his "species book" [6,7] is based on the implicit assumption that the Earth is a static planet.

Today it is well established by numerous independent studies that (1.) bacteria are, based on their collective protoplasmic biomass, the dominant forms of life, and by no means "primitive", (2.) endosymbiotic processes due to the fusion of ancient microbes have been key events in the history of life, and (3.) the Earth is not static, but dynamic. Our post-Darwinian view of the symbiogenetic and dynamic tree of life is described in the next sections.

Ernst Haeckel's static trees and the origin of Monerology

In Germany, the zoologist Ernst Haeckel (1834-1919) was one of the most prominent popularizers of Darwin's ideas, notably of his "theory of descent with modification by means of natural selection" (i.e., the concepts 1. and 5. depicted in Figure 4). It should be noted that, in contrast to many of his colleagues, Haeckel fully acknowledged the achievements of Jean Lamarck. In one of his popular books, Haeckel argued that the term "Lamarckism" should be used to denote the principle of the transformation of species (i.e., evolution as such, corresponding to Darwin's theory no. 1), whereas the word "Darwinism" should denote the concept of natural selection, one of the British biologist's most important insights and contributions to the developing evolutionary sciences of the 19th century [20,26].

With respect to the "Tree of Life" as a coral-like structure (Figures 3 and 4) it should be remembered that Haeckel discovered and later described a marine coral from the Red Sea that was named after his friend and colleague Charles Darwin. A drawing of this organism (*Monoxenia darwinii* Haeckel 1876) is shown in Figure 5 A. One of Haeckel's greatest and most original contributions to evolutionary biology, his "Gastraea-Theorie", was based on his detailed investigations of the development of "Darwin's coral" (*Monoxenia darwinii*). In a journal article published in 1874 (two years before the organism *M. darwinii* was described as a new species), Haeckel concluded that the two-layered gastrula (i.e., the "Gastraea" or "Urdarmtier") is the ancestral form of all animals. This is the essence of Haeckel's Gastraea theory for the origin of the Metazoa (multicellular animals) [27], a concept that has been corroborated by numerous subsequent studies.

In Vol. 2 of his *Generelle Morphologie der Organismen* published in 1866, Haeckel outlined his "biogenetic law", which the author later described in more detail, in the following words: "Ontogenesis is the short and fast recapitulation of phylogenesis, controlled through the physiological functions of inheritance (reproduction) and adaptation (nutrition)" [28]. The significance of Haeckel's

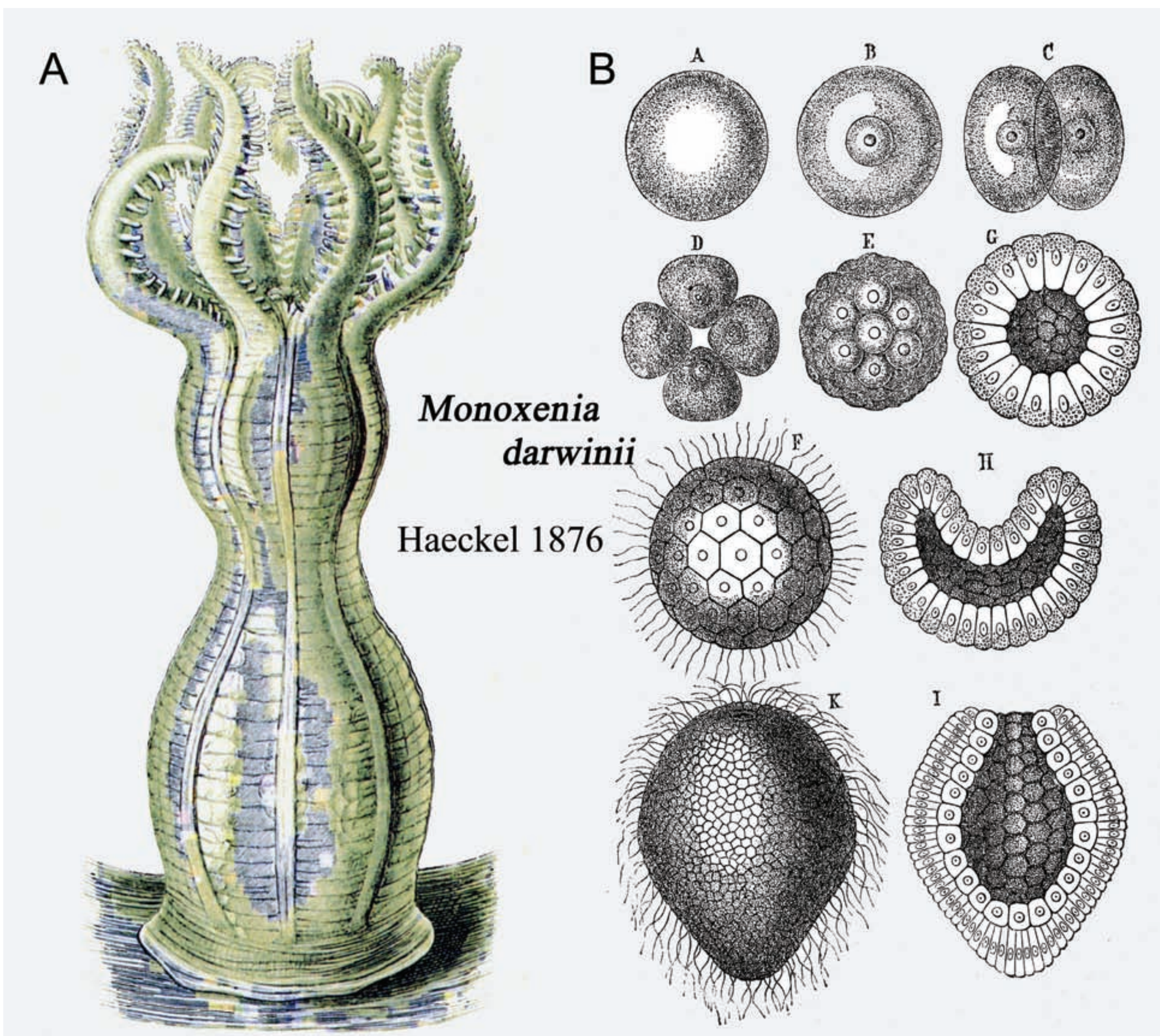

Figure 5 Adult specimen of "Darwin's coral" and ontogenesis of Haeckel's model system. Morphology of the coral *Monoxenia darwinii* (A), an organism discovered by Ernst Haeckel in 1873 in the Red Sea and later described by him as a new species, named in honour of Charles Darwin. The development of *M. darwinii* is shown in (B), from the fertilized egg (*A/B*) to the so-called "Becherlarve" (beaker larvae) or gastrula (*K/I*). Haeckel coined the term "Gastraea" to denote this phylogenetically conserved stage in animal development [adapted from ref. 27].

"law" (which is today down-sized to a "rule" that permits exceptions), with respect to the evolution of animals, has recently been described by Olsson et al. [29]. More importantly within the context of this article are the "genealogical trees" drawn and depicted by Haeckel in his classic monograph. In all of these tree-like diagrams, German oaks were used as the representative woody plant. This choice is not surprising. According to the pre-Darwinian idea of the *Scala Naturae* (Figure 2), the one primate of plants, organisms that were ranked in this Christian medieval hierarchy below the animals, were oak trees [10]. Since the British scientist Wallace likewise referred to the "twigs of a gnarled oak" [19], we have to conclude that so-called "ladder-thinking" was still alive in the minds of Haeckel and Wallace, who published major books on organismic evolution after the death of Darwin in 1882.

The most prominent "general" evolutionary tree of Haeckel, depicting the presumed phylogenetic relationships between animals, plants and various "lower organisms" is reproduced in Figure 6. Three facts should be highlighted in this context. First, Haeckel [28] argued that the "Stammbaum der Organismen" (Tree of Life) is monophyletic. This hypothesis, which corresponds to Darwin's "species theory No. 2" (see Figure 4), has recently been corroborated by D. J. Theobald [30], based on protein sequence and other molecular data. The author concluded that "the last universal common ancestor [LUCA] may have comprised a population of organisms with different genotypes that lived in different places at different times" [30]. Second, in contrast to Darwin [6,7], whose work was based on the 19th-century "animal-plant-classification", Haeckel distinguished between three "Kingdoms of life":

1. Archephylum vegetabile (Plantae), 2. Archephylum protisticum (Protista), and 3. Archephylum animale (Animalia). Hence, unicellular "lower organisms" (Protista, inclusive of the Moneres, i.e., Bacteria), living beings that were largely ignored by Darwin [6,7], were present in Haeckel's view of biodiversity on Earth. Finally, Haeckel [28] coined the term "Moneres autogonum" to denote micro-organisms at the common root ("Radix communis Organismorum") of his "Tree of Life" (Figure 6). However, it should be noted that on other pages of his books, Haeckel [28] refers to polyphyletic origins of species. A discussion of all of Haeckel's pertinent ideas is beyond the scope of this article.

The inclusion of microbes that lack a true nucleus ("Moneres autogonum") into an evolutionary scheme was a large step towards our modern view of biodiversity. Today we know that the moneres (Kingdom Bacteria or Monera) are the dominant forms of life on Earth [31]. It is obvious that, via the inclusion of the Protista (i.e., micro-organisms with and without a nucleus), Haeckel [28,32] tremendously enlarged our view of life on Earth - the discipline of "Monerology" (i.e., Bacteriology and Protozoology) with respect to evolutionary questions rests to a large extent on the work of this famous German biologist. In some of his later writings, Haeckel mentioned the principle of endosymbiosis (or symbiogenesis), with reference to the origin of certain green algae. This topic is discussed in the next section.

Constantin Mereschkowsky's symbiogenesis theory and the origin of eukaryotes

In a seminal paper published a century ago in German, the Russian biologist Constantin Mereschkowsky (1855-1921) wrote that the most important question of the biological sciences concerns the origin of species on Earth. However, according to Mereschkowsky [33], earlier attempts of Darwin and Haeckel were not successful, because "at the time when they were active not all the facts that are necessary to solve this problem were available. However, in the meantime novel facts from disciplines such as cytology, biochemistry, physiology, notably of the lower organisms, accumulated so that a new approach to solve the riddle concerning the origin of living beings is justified" [33].

As an alternative to the Darwinian principle of "descent with modification (i.e., biological evolution) by means of natural selection", Mereschkowsky proposed his theory of symbiogenesis [34,35]. This concept posits that new organisms, at the level of single cells, occur via symbiotic events, i.e., by means of the fusion and subsequent cooperation of microbes or "Moneren". Since the origin of the nucleus was one of Mereschkowsky's major topics, the term "symbiogenesis" includes "eukaryogenesis", i.e., the evolutionary development of nucleated cells from non-nucleated, bacteria-like ancestors. Hence, the original word "symbiogenesis" should be used instead of the more recently introduced term "eukaryogenesis" to denote those processes that led to the origin of the earliest nucleated (eukaryotic) cells [35].

Based on Mereschkowsky's insights and those of other cytologists, L. Margulis proposed the "serial endosymbiosis hypothesis of the origin of eukaryotic cells" that contain a nucleus and organelles (mitochondria, chloroplasts) within their cytoplasm [36,37]. The evidence for this version of the "symbiogenesis theory" has been summarized and discussed at length by Kutschera and Niklas [38,39], Cavelier-Smith [40-43], Koonin [44-47] an others [48,49]. As E. Koonin has recently stated in this journal, according to the well-supported "symbiogenesis sceniario", a single endosymbiotic event involving the uptake and subsequent domestication/enslavement of an alpha-proteobacterium by an archaebacterial host cell led to the generation of the mitochondria within heterotrophic eukaryotic cells. In a second step, the uptake of an ancient cyanobacterium, led

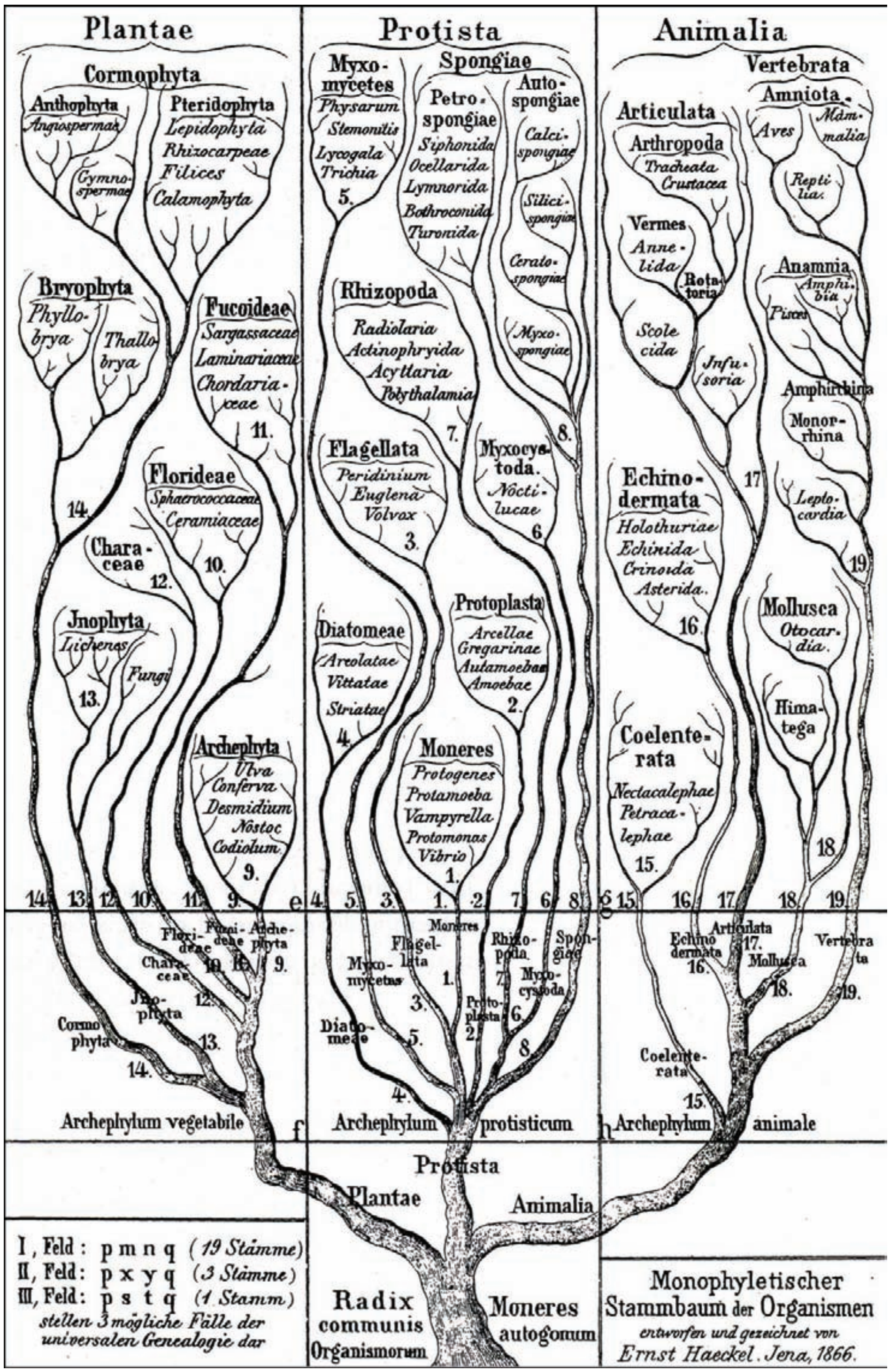

Figure 6 Reproduction of Ernst Haeckel's genealogical oak tree depicting the Kingdoms Plantae (plants), Protista (micro-organisms) and Animalia (animals). Note that the author explicitly pointed out that this general Tree of Life is monophyletic [adapted from ref. 28].

to the origin of plastids (chloroplasts) [44]. These key events in the history of life on Earth (i.e., serial primary endosymbioses 1 and 2) occurred ca. 2200 to 1500 and ca. 1500 to 1200 million years ago, respectively, during the Palaeo- and Mesoproterozoic [38]. At that time, the oxygen content of the oceans was about to rise due to cyanobacterial photosynthesis. Gross and Bhattacharya [50] have proposed that the "birth of eukaryotes, a milestone in the evolution of life on our planet", was driven by the selective pressure caused by reactive oxygen species (ROS). These ROS were light-mediated by-products of the local rise in O_2-levels within marine ecosystems during the Proterozoic.

Although many details concerning the evolutionary origin of the earliest nucleated, organelle-containing cells are still a matter of debate [51-53], there is agreement among scientists that symbiogenesis (primary endosymbiosis) was an early key process in the history of life [38,39,54]. However, although Mereschkowsky [33] was the first to clearly point out the importance of endosymbiotic events during evolution, he did not accept the "Darwin-Wallace principle of natural selection" [20] as a driving force for the transformation of species. This idea prevails to the present day: a number of "symbiogenesis-researchers" consider endosymbiotic events and directional natural selection as mutually exclusive concepts (see ref. 38 for a discussion of this topic). However, as documented in detail elsewhere [26,54,55], this view of the natural world is at odds with numerous observations and experiments. Symbiogenesis, i.e., primary (and secondary) endosymbioses, combined with directional natural selection caused by slowly changing environmental conditions, have been two key processes or "driving forces" of organismic evolution, since the origin of the hypothetical Last Universal Common Ancestor (LUCA) that gave rise to a heterogeneous population of aquatic, bacteria-like Proto-cells ca. 3800 million years ago [24,30]. These "factors" of biological evolution, with respect to the "Tree of Life", are depicted in Figure 7.

It should be noted that the relevance of endosymbiotic events, combined with the process of (bacterial) horizontal gene transfer, has already been discussed with reference to the "Tree of Life" [23-25,42,56]. However, a third key process shown in Figure 7, the movements of tectonic plates (i.e., the dynamic Earth), has been ignored by these investigators. The significance of these gradual (sometimes abrupt) changes in the environment with respect to biological evolution are discussed in the next section.

Alfred Wegener's vision of the dynamic Earth, volcanism and plate tectonics

Four decades ago, J. C. Maxwell summarized the concept of the dynamic Earth in the following words: "The earth's surface, in the context of geologic time, may be likened to a boiling vat of maple syrup. The crust, with its high-standing continents, is analogous to the scum which rises from boiling syrup, coalesces, drifts apart, and rejoins in different patterns on the surface of the convecting liquid. The earth's crust is a similarly thin scum of relatively light rocks 'floating' on the mantle, a zone of heavier materials extending halfway to the earth's center and overlying the inner metallic core. By some cosmic accident the earth has been endowed with a magnetic field, apparently for much of its 4.5-billion-year history.

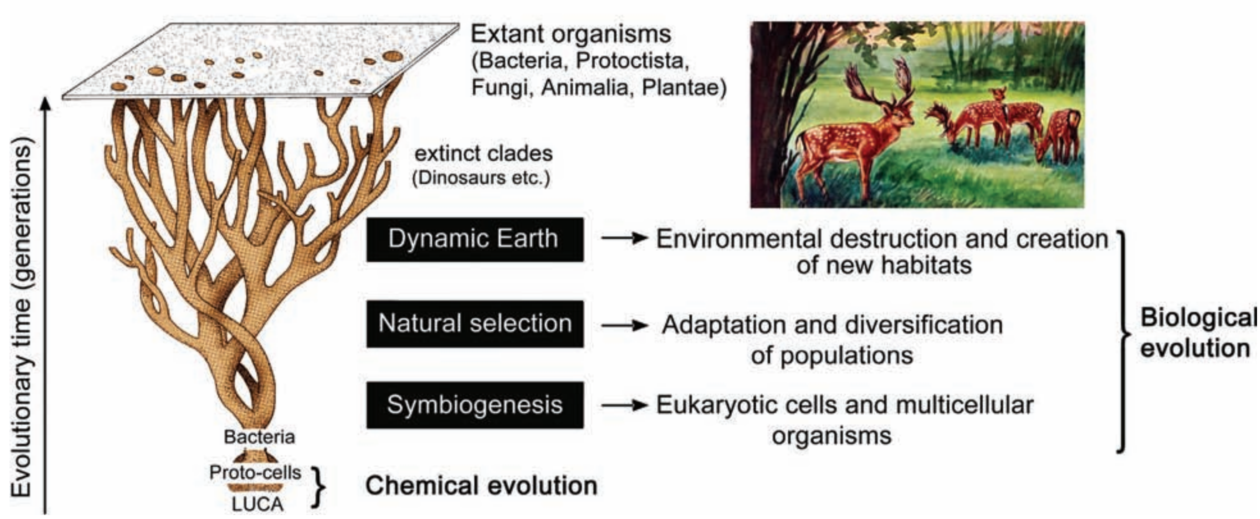

Figure 7 Symbiogenesis, natural selection, and the dynamic Earth as key processes that caused biological evolution. The Last Universal Common Ancestor (LUCA) evolved into the earliest self-replicating proto-cells (ancient microbes) ca. 4000 to 3500 million years ago. Over the subsequent eons, these archaic microbes evolved into numerous bacterial ecotypes that today inhabit every micro-niche where organic molecules (or light) are available. Moreover, these micro-organisms gave rise to larger, eukaryotic cells via symbiogenesis (primary endosymbiosis). These nucleated cells further evolved into multicellular organisms, such as algae, fungi, animals and plants.

Changes in the field with respect to a point on the surface are recorded by successively formed sequences of rock. Analysis of these ancient magnetic fields gives convincing evidence of extensive differential movements in the earth's crust. The composition of the crust and the forces which cause its deformation are apparently determined by gravitational and thermal instabilities within the outer few hundred kilometers of the mantle. Temperature within the earth increases downward at a rate exceeding the adiabatic gradient for the upper few hundred kilometers, hence this outer zone is intrinsically unstable. Vertical movements, once initiated, tend to be self-propagating. These instabilities may give rise to lateral and vertical movements approximating convecting currents in liquids. Rising currents have apparently occurred largely in oceanic areas, bringing new mantle material to the surface in the oceans and sweeping older oceanic rocks towards and perhaps beneath the high-standing continents. The great mountain ranges which border many continents are believed to be related in some way to the convective overturn of rocks in the earth's crust and upper mantle" [57]. This description, published in 1971, was a concise summary of a long series of articles and books that originated in 1858.

In this year, the French geographer Antonio Snider-Pellegrini (1802-1885) published two imaginative maps depicting the continents of the Earth, "before and after separation" [58]. This early outline of the idea of continental drift, and hence the dynamic Earth (Figure 8 A), did not convince the geologists of the time, because Snider-Pellegrini's speculations were largely based on Biblical myths and only on few scattered empirical data. As a result, the old concept of a static Earth, the "geological basis" of all views of the "hierarchy and organization of life on our planet", as depicted in ladders and trees, from Charles Bonnet's *Scala* via Darwin's *Diagram* to Ernst Haeckel's *Oak*, prevailed (Figures 1 to 6).

Seven decades after Snider-Pellegrini's account was published, the last (definitive) edition of Alfred Wegener's (1880-1930) book on *The Origin of the Continents and the Oceans* [59] appeared in print. In this monograph of 1929, the German scientist summarized a long list of empirical evidence for a novel fact-based theory of continental drift that overshadowed the earlier, Bible-inspired speculations of the French geographer. In essence, Wegener stated that the isolated continents as we observe them today were once united and formed a super-continent. This giant proto-land mass ("Pangaea") may have covered up to 50% of the surface of our planet and was surrounded by one large ocean ("Panthalassa"). Due to "continental drift" via mechanisms inexplicable to Wegener, the land masses finally reached, in the course of millions of years of steady motion, the position they have today. Despite Wegener's inability to explain the physical processes that may have caused the drift of these large land masses, the author proposed that the formation of mountains, via compressive forces, the occurrence of earthquakes, and volcanism are consequences of continental drift [59]. Today it is well established that Wegener was right (Figures 8 B, C; 9).

Only a few years before J. C. Maxwell published his summary of the "Dynamic Earth" quoted above, the concept of plate tectonics was proposed. This unifying theory of geology states that the Earth's outer rigid shell (i.e., the lithosphere) is broken into more than a dozen giant, rigid plates that float on the hot, ducile mantle (i.e., the asthenosphere) like pieces of ice on a lake. Most of the Earth's documented history results from plates rifting into pieces to form new ocean basins. When they converge back together, they can form mountains and large continents (Figure 8 C). As shown in Figure 9, the rigid lithospheric plates differ in size and their direction of internal heat-driven motion. Some pieces of the outer crust, such as the North American Plate, carry continents and attached pieces of the ocean floor. Other parts of the lithosphere, such as the Pacific Plate, are entirely covered by oceans and are made of oceanic crust. For instance, in the area of San Francisco (California) and elsewhere, the North American and Pacific Plates are pushed at each other, and the spontaneous release of pressure causes abrupt, short plate movements, so-called "earthquakes" (Figure 8 B). These rapid, unpredictable geologic events may have devastating secondary effects. For instance, the 2011 Sendai 9.0 megathrust earthquake that occurred on March 11 off the coast of Japan triggered destructive tsunami waves with highs of up to 12 m. These masses of sea water have travelled up to 10 km inland, destroyed the terrestrial landscape, and caused thousands of deaths. Frequently, such devastating earthquakes occur along the so-called "Pacific Ring of Fire", stretching from New Zealand, along the eastern edge of Asia north across the Aleutian Islands of Alaska and south along the coast of North and South America. The "Ring of Fire", which has 452 volcanoes, is a direct consequence of plate tectonics and hence the movements/collisions of crustal plates [60].

What is the significance of the theory of plate tectonics for the geological sciences? Theodosius Dobzhansky (1900-1975) once said that "Nothing in biology makes sense except in the light of evolution" [61]. Accordingly, earth scientists may conclude that "Not much in geology makes sense except in the light of plate tectonics". In other words, the theory of plate tectonics is the unifying principle of historical geology.

The consequences of the internal heat-driven movements of tectonic plates for the evolution of life on Earth, as well as the "Tree-models" depicting this process, are obvious: new habitats are created and existing

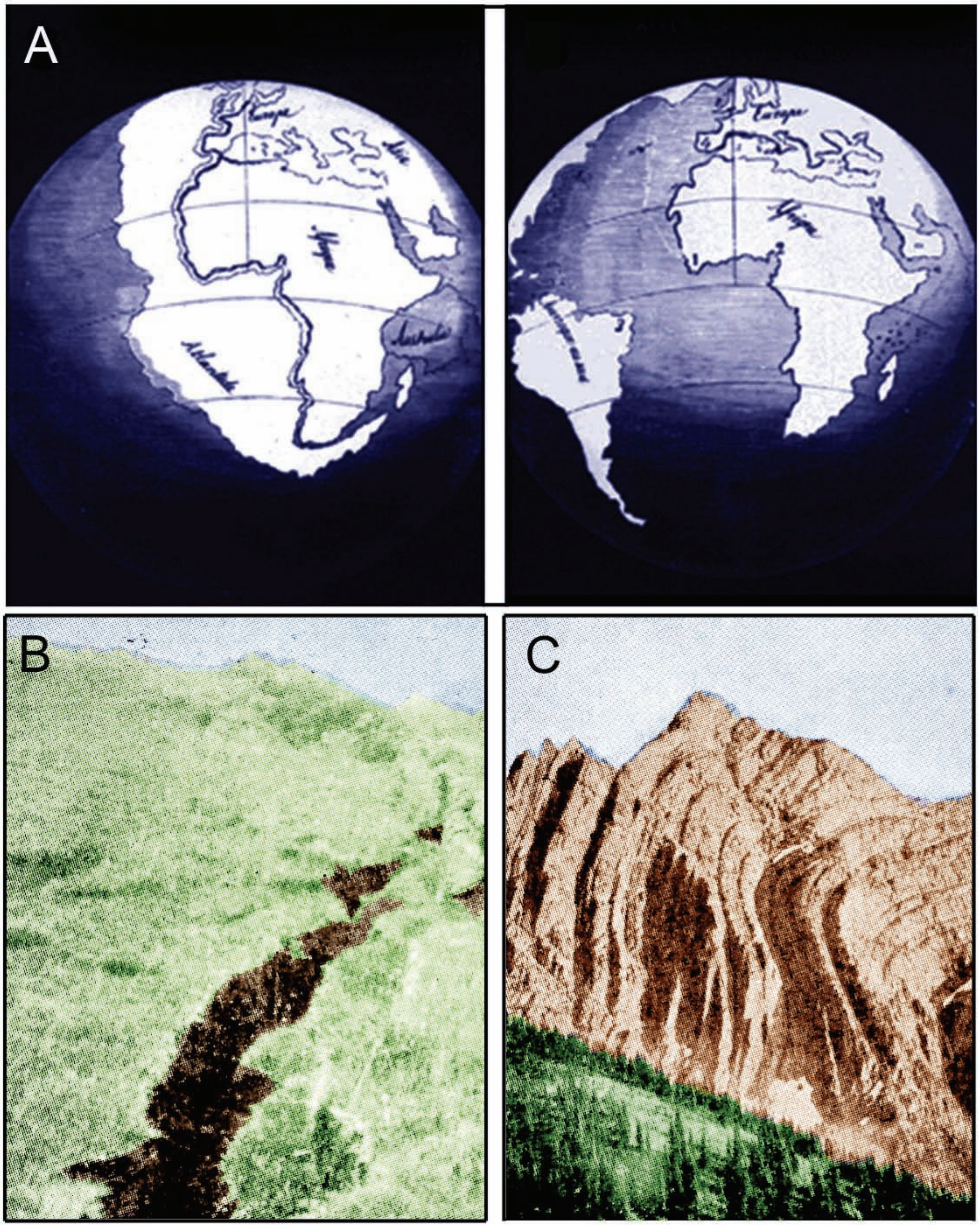

Figure 8 Scheme depicting the idea of continental drift as envisioned by A. Snider-Pellegrini in 1858 (A). This concept was re-discovered and supported by empirical evidence by A. Wegener in 1929. Decades later, the theory of plate tectonics was deduced. Plate tectonics accounts for most of the planet's earthquakes, which may result in deep cracks in the Earth's surface (B) and the formation of mountains as a result of horizontal compression of the crust (C) [adapted from ref. 58 and from photographs of the US Geological Survey, 1938].

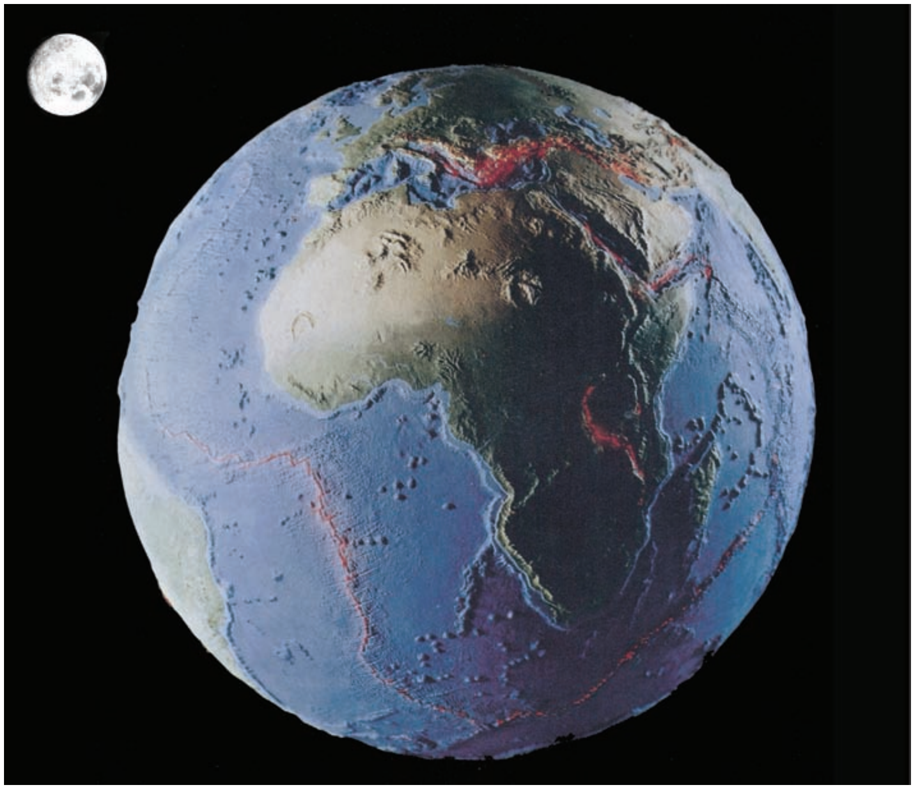

Figure 9 Model of the Earth's surface, which is broken into drifting fragments, the so-called tectonic plates. The "lubricant" of plate movements is liquid water. In this picture, the South American and African plates are highlighted. In addition, the moon, a solid satellite without water and plate movements, is shown in the upper left quarter. Red lines: Regions where volcanic eruptions occur frequently [adapted from ref. 75].

ones are re-modelled or destroyed by these geologic events (Figure 7). Major mass extinctions, such as those that occurred 251 and 65 million years ago, respectively, were at least in part caused by massive volcanic eruptions and hence the dynamic Earth [54,60].

In a recent publication it was documented that the break-up of the super-continent Pangaea (which existed from the Perminan into the Jurassic, ca. 299 to 200 million years ago), due to plate tectonics, accounts for the evolutionary diversification of many groups of animal, such as dinosaurs, mammals and the land leeches of Madagascar [62]. Another example for the role of plate tectonics as driving force for speciation are amphibious tetrapods, such as salamanders. A detailed analysis of numerous collected specimens of the four-toed Asian salamanders (family Hynobiidae) revealed that the 46 biospecies were "created" as a result of plate tectonics. About 110 million years ago, much of Asia was a low-lying humid region where salamanders of all varieties existed. A series of geologic events, which resulted in the lifting up of the Tibetan Plateau and mountain-building led to the isolation of sub-populations that evolved, over millions of years, into separate, geographically isolated species [63]. Hence, the dynamic Earth must be interpreted as a major factor that drove the evolutionary diversification of many macro-organisms on our planet [64,65] (Figures 8, 9). It should be mentioned that wildfires, which have a large impact on the distribution and diversification of plants and animals, are regularly caused by massive volcanic eruptions (Figures 10, 11). These secondary consequences of plate tectonics may also have been an important cause for the extinction of the dinosaurs that occurred 65 million years ago [54,61,66].

Finally, we have to address the question as to the consequences of volcanism (and the associated wildfires) on the evolutionary patterns of micro-organisms, such as bacteria, soil amoebae and unicellular algae (diatoms etc.) [67]. One case study may illustrate this topic. The eruption of Mount St. Helens in southwest Washington, USA, on May 18, 1980 released superheated steam and gases. Moreover, this catastrophic event resulted in pyroclastic flows, landslides, mudflows, and ash fall. As a result, novel habitats were formed, whereas old ones were re-structured, scoured, or eliminated [68]. Six years after the eruption, some aquatic habitats were

Figure 10 The massive 1872 eruption of the Vesuvius, the only active volcanoe in mainland Europe (Italy). Vesuvius is most famous for the 79 A. D. eruption that destroyed the Roman cities of Pompeii and Herculaneum. Plate tectonics is the major cause for these violent eruptions, which document ongoing magmatic processes driven by heat from the radioactive decay within the Earth [adapted from an anonymous painting, ca. 1880].

analyzed with respect to the presence of micro-organisms. The results show that species richness and microbial diversity were very low at the most heavily disturbed sites around the cool volcano, documenting a large mass extinction event at the "micro-scale" [69]. However, more work on other volcanic sites is necessary to corroborate these results. These data document that volcanic eruptions (and wildfires) lead to a temporary "sterilisation" of the affected aquatic and terrestrial habitats and hence to the destruction of most of the micro-organisms that existed there before the catastrophic event occurred (Figures 10, 11). The patterns of re-colonization by microbial communities and the resulting evolutionary diversifications are not yet explored in detail.

Conclusions: The tree-like Synade-model of macroevolution

In a recent analysis of Charles Darwin's "species book" it was documented in detail that the British naturalist and theologian used Biblical phrases such as "He who ..." throughout his *Origin of Species* [70]. Darwin's key metaphor for the principle of descent with modification, combined with his theory of the last common ancestor, was the "great Tree of Life" [6,7]. In this context I would like to add that the symbol of Trees appears in the creation myth of the Old Testament (Genesis 2, 9): "And the Lord God made all kinds of trees grow out of the ground - trees that were pleasing to the eye and good for food. In the middle of the garden were the tree of life and the tree of the knowledge of good and evil".

In this article I have shown that, from the earliest, Bible-inspired "Moral Tree" (Figure 1), via the hierarchical *Scala Naturae*, to Darwin's and Haeckel's static trees (or corals) of life, the old, Biblical "woody plant-model" evolved by descent with modification: The Christian "ladder-thinking" was gradually replaced by the post-Darwinian ("Haeckelian") atheistic "oak-tree-concept" that included animals, plants and micro-organisms (Figure 6). However, neither Darwin nor Haeckel took the principle of symbiogenesis (primary endosymbiosis) into account, because this evolutionary process - the "creation" of more complex eukaryotic cells via the fusion of archaic microbes and the subsequent cooperation of the partners - was largely unknown at that time. It should be stressed that Haeckel mentioned symbiogenetic events in the context of the origin of green algae and land plants [34], but the German biologist failed to integrate this insight into his general picture of the evolution of life on Earth.

Moreover, the trees of Darwin and Haeckel are "static", based on their implicit assumption of an Earth surface that does not display significant movements. Unfortunately, even the "architects" of the Synthetic

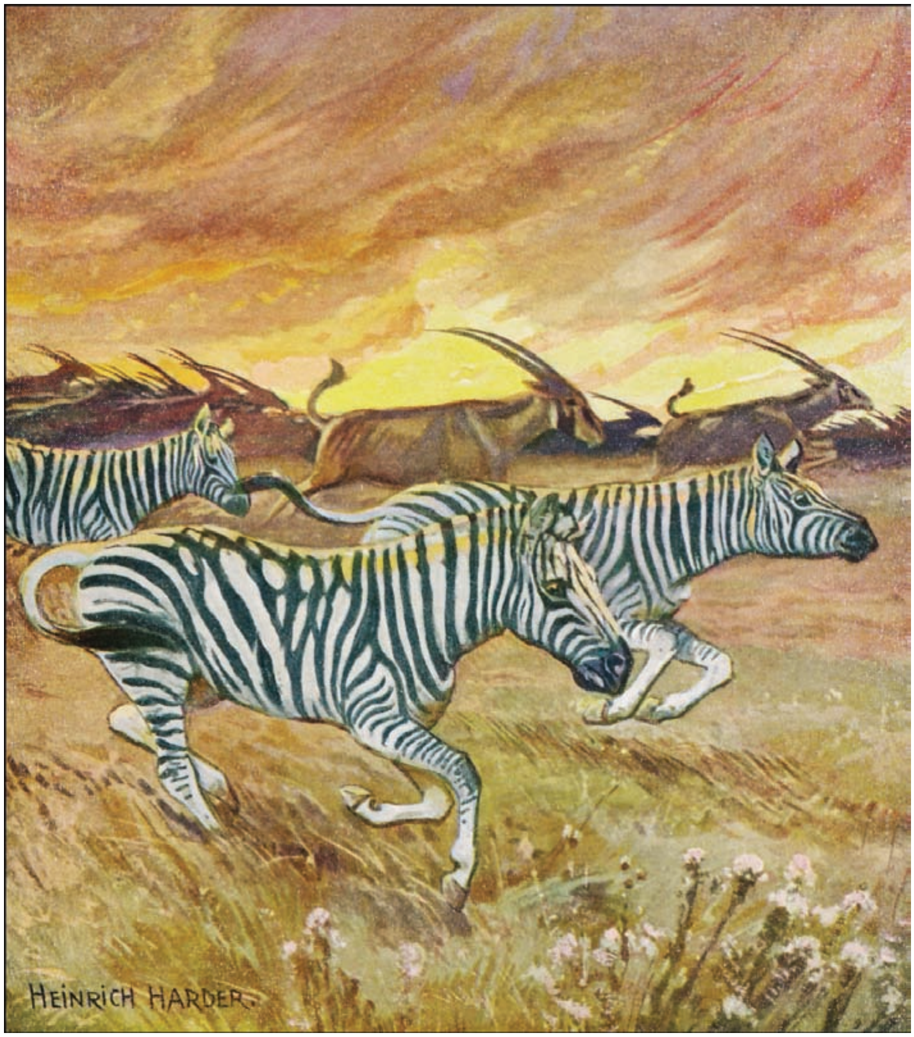

Figure 11 Volcanic eruptions can ignite wild fires that result in the destruction of the vegetation, soil micro-organisms, and less mobile animals. In this drawing, Zebras and other mammals are depicted that are just about to escape from a severe wild fire [adapted from a drawing of H. Harder, 1912].

Theory of Biological Evolution developed between 1937 and 1950, Theodosius Dobzhansky (1900-1975), Ernst Mayr (1904-2005), Julian Huxley (1887-1975), George G. Simpson (1902-1984), Bernhard Rensch (1900-1990), and G. Ledyard Stebbins (1906-2000) ignored symbiogenetic events and the dynamic Earth [54,61,71-73]. These fundamental processes were, like the insights gained from the disciplines of evolutionary developmental biology ("Evo-Devo") and geology (mass extinctions), integrated into the "Expanded Synthesis" published in 2004 [54,74]. Due to this steady growth of our "Tree of modern evolutionary knowledge", the scientific discipline of evolutionary biology has been defined as a "system of theories" that explains the various aspects of those processes that Charles Darwin described as "descent with slight and successive modifications" [6,7].

W. F. Doolittle [23-25,56] and others [52] have recently argued that the construction of a universal Tree of Life, as originally suggested by Darwin [6,7] and Haeckel [28] (Figures 4 and 6), may be difficult to achieve. These authors based their judgement on two facts. First, in prokaryotes (bacteria, cyanobacteria), which comprise the majority of life forms on Earth and were the sole organisms during ca. 2/3 of the early history of organismic evolution on this planet, lateral gene transfer (the exchange of genetic information between extant microbes) occurs regularly. Second, endosymbiotic events, and hence the fusion of microbial lineages, should be taken into account when tree-like models are drawn [51].

In my view, symbiogenesis, denoted here as early primary endosymbiotic processes that gave rise to the organelle-bearing eukaryotic cells during the Proterozoic, and subsequent, secondary endosymbiotic events that are responsible for the origin of the majority of the unicellular marine phytoplanktonic organisms [38,39,54,74], were key events during the history of life. Moreover, plate tectonics and hence the dynamic Earth must be incorporated into our view of any tree-like reconstruction of biological evolution. Based on the facts summarized in this article and elsewhere [5,62,75] I propose that symbiogenesis, (directional) natural selection, and the dynamic Earth were key processes that must be viewed as three important "driving forces" of organismic evolution (Figure 7).

A more precise "tree-like" version of this "synade-model" of macroevolution, which takes into account all organisms on Earth (i.e., members of the Kingdoms Bacteria, Protoctista, Animalia, Fungi, and Plantae) is depicted in Figure 12. The oldest branch of living beings, the Bacteria (syn. Kingdom Monera), represent more than 50% of the protoplasmic biomass on Earth [31]. They are, as pathogens and/or symbionts, important "factors" in the evolution of all Eukaryotes. Hence, ancient and recent prokaryotic microbes are included as "background organisms" [31,67]. In addition, a scheme of our planet depicting the centre of the Earth is shown in Figure 12. Without internal heat, which is primarily caused by the energy given off as a result of the radioactive decay of uranium, our "blue planet" would probably be as static as the moon (Figure 9).

According to the "tree-like" synade-model of macroevolution proposed here (Figures 7 and 12), all extant and extinct organisms have, through the eons of geological time, benefited from the dynamic Earth due to the creation of early terrestrial land masses within giant marine habitats, and the subsequent formation of mountains, deserts, freshwater ecosystems, and deep oceans [64,75]. On the other hand, massive volcanic eruptions, which are "side effects" of plate tectonics, have caused (or significantly contributed to) several mass extinctions during Earth's history. Hence, the mobile tectonic plates led to the destruction of countless living beings on this "blue planet of the microbes". Finally, it should be stressed that micro-organisms, the "unseen majority" [31] that Darwin largely ignored [76,77], are the true "winners" in the ongoing, ca. 3.500 million-year-long "struggle for life" on our ever changing, dynamic Earth [5,59-62,78-86].

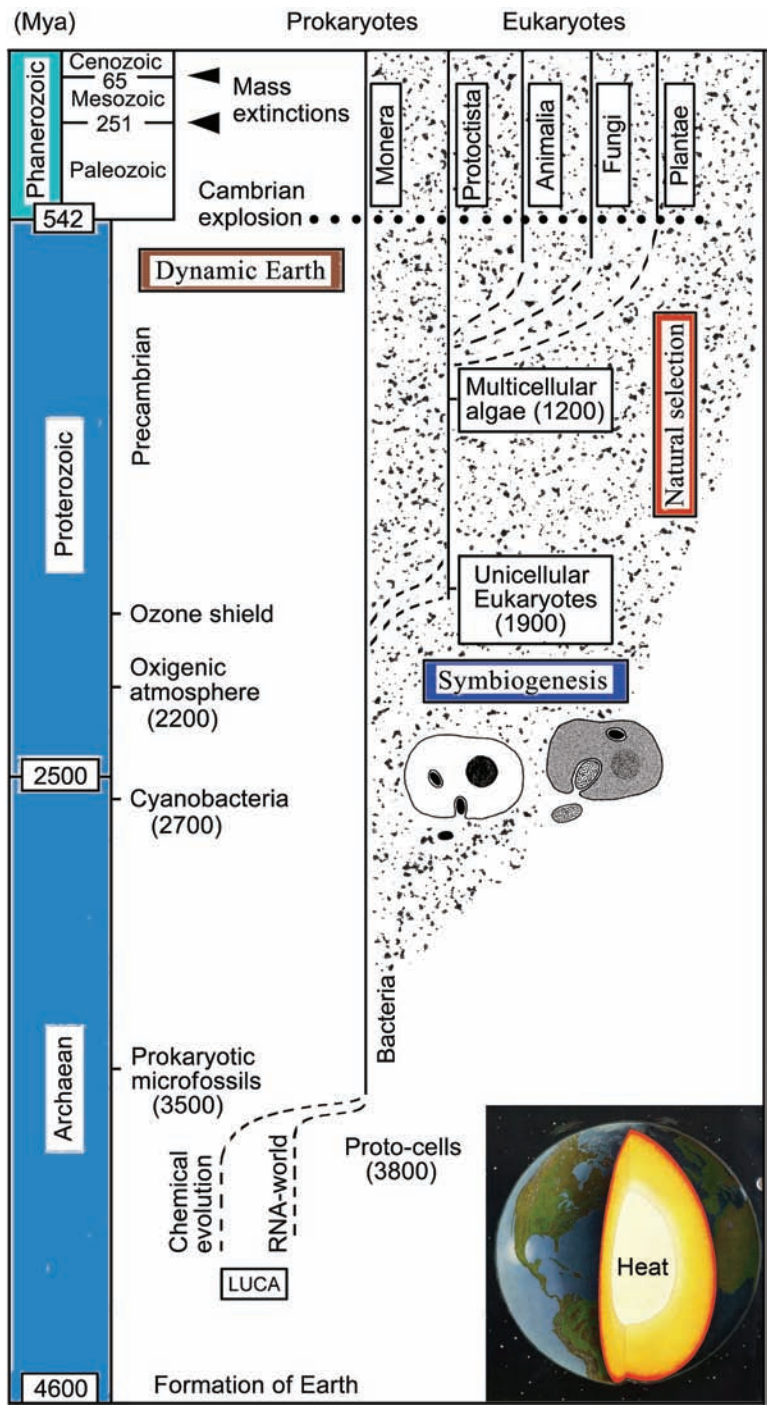

Figure 12 The tree-like "Synade-model of macroevolution", taking into account all five Kingdoms of life on Earth. According to this theory, symbiogenesis (primary and secondary endosymbiotic events), (directional) natural selection, and the (internal heat-driven) dynamic Earth were and still are key drivers of macroevolution on our "planet of the bacteria" [adapted and modified from ref. 62].

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Authors' contributions
The author planned and wrote the paper.

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References

1. Barlow N, (ed.): *The Autobiography of Charles Darwin* London: Collins; 1958.

2. Kutschera U, Niklas KJ: **Evolutionary plant physiology: Charles Darwin's forgotten synthesis.** *Naturwissenschaften* 2009, **96**:1339-1354.
3. Kutschera U, Briggs WR: **From Charles Darwin's botanical country-house studies to modern plant biology.** *Plant Biol* 2009, **11**:785-795.
4. Kutschera U, Elliott JM: **Charles Darwin's observations on the behaviour of earthworms and the evolutionary history of a giant endemic species from Germany, *Lubricus badensis* (Oligochaeta: Lumbricidae).** *Appl Environm Soil Sci* 2010, **2**:1-11.
5. Kutschera U: **Charles Darwin's *Origin of Species*, directional selection, and the evolutionary sciences today.** *Naturwissenschaften* 2009, **96**:1247-1263.
6. Darwin C: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* London: John Murray; 1859.
7. Darwin C: *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* 6 edition. London: John Murray; 1872.
8. Kearney H: *Science and Change 1500-1700* New York and Toronto: World University Library; 1971.
9. Bonner A, (ed.): *Doctor Illuminatus: A Ramon Lull Reader* Princeton: Princeton University Press; 1985.
10. Bynum WF: **The Great Chain of Being after forty years: An appraisal.** *History of Science* 1975, **13**:1-28.
11. Mayr E: *The Growth of Biological Thought. Diversity, Evolution, and Inheritance* Cambridge, Massachusetts: Harvard University Press; 1982.
12. Mayr E: *What Evolution Is* New York: Basic Books; 2001.
13. Junker T, Hoßfeld U: *Die Entdeckung der Evolution.* 2 edition. Auflage. Darmstadt: Wissenschaftliche Buchgesellschaft; 2009.
14. Ragan MA: **Trees and networks before and after Darwin.** *Biol Direct* 2009, **4**:43.
15. Bonnet C: In *Oeuvres d'histoire naturelle et de philosophie. Volume 1.* Neuchatel; 1779.
16. Lamarck J-B: *Philosophie Zoologique, ou Exposition des Considérations relatives à l' Histoire naturelle des Animaux* Paris: Dentu et 'l Auteur; 1809.
17. Lamarck JB: *Histoire Naturelle des Animaux sans Vertèbres* Paris: Verdière; 1815.
18. Koonin EV, Wolf YI: **Is evolution Darwinian or/and Lamarckian?** *Biol Direct* 2009, **4**:42.
19. Wallace AR: **On the law which has regulated the introduction of new species.** *Ann Mag Nat Hist (n s)* 1855, **16**:184-196.
20. Kutschera U: **Darwin-Wallace principle of natural selection.** *Nature* 2008, **453**:27.
21. Darwin E: In *Zoonomia; or the Laws of Organic Life. Volume 1 to 3.* Boston: Thomas & Andrews; 1794.
22. Bredekamp H: *Darwins Korallen Die frühen Evolutionsdiagramme und die Tradition der Naturgeschichte* Berlin: Verlag Klaus Wagenbruch; 2005.
23. Doolittle WF: **The practice of classification and the theory of evolution, and what the demise of Charles Darwin's tree of life hypothesis means for both of them.** *Phil Trans R Soc Lond B: Biol Sci* 2009, **364**:2221-2228.
24. Doolittle WF: **Phylogenetic classification and the universal tree.** *Science* 1999, **284**:2124-2128.
25. Doolittle WF: **The attempt on the life of the Tree of Life: science, philosophy and politics.** *Biol Philos* 2010, **25**:455-473.
26. Kutschera U: **A comparative analysis of the Darwin-Wallace papers and the development of the concept of natural selection.** *Theory Biosci* 2003, **122**:343-359.
27. Haeckel E: **Die Gastraeatheorie, die phylogenetische Classification des Thierreiches und die Homologie der Keimblätter.** *Jena Z Naturwiss* 1874, **8**:1-55.
28. Haeckel E: *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenztheorie. Bd. 1 und 2* Berlin: De Gruyter; 1866.
29. Olsson L, Levit GS, Hoßfeld U: **Evolutionary developmental biology: its concepts and history with a focus on Russian and German contributions.** *Naturwissenschaften* 2010, **97**:951-969.
30. Theobald DL: **A formal test of the theory of universal common ancestry.** *Nature* 2010, **465**:219-222.
31. Whitman WB, Coleman DC, Wiebe WJ: **Prokaryotes: the unseen majority.** *Proc Natl Acad Sci USA* 1998, **95**:6578-6583.
32. Haeckel E: *Das Protistenreich. Eine populäre Übersicht über das Formengebiet der niedersten Lebewesen. Mit einem wissenschaftlichen Anhang: System der Protisten* Leipzig: Ernst Günther; 1878.
33. Mereschkowsky C: **Theorie der zwei Plasmaarten als Grundlage der Symbiogenesis, einer neuen Lehre von der Entstehung der Organismen.** *Biol Zentralblatt* 1910, **30**:278-303.
34. Sapp J, Carrapico F, Zolotonosov M: **Symbiogenesis: The hidden face of Constantin Merezhkowsky.** *Hist Phil Life Sci* 2002, **24**:413-440.
35. Geus A, Höxtermann E: **Evolution durch Kooperation und Integration. Zur Entstehung der Endosymbiosetheorie in der Zellbiologie.** Basilisken-Presse, Marburg; 2007, (Hg).
36. Margulis L: **Symbiosis in Cell Evolution.** *Microbial Communities in the Archean and Proterozoic Eons.* 2 edition. New York: W. H. Freeman & Co; 1993.
37. Margulis L: **Archaeal-eubacterial mergers in the origin of Eukarya: Phylogenetic classification of life.** *Proc Natl Acad Sci USA* 1996, **93**:1071-1076.
38. Kutschera U, Niklas KJ: **Endosymbiosis, cell evolution, and speciation.** *Theory Biosci* 2005, **124**:1-24.
39. Kutschera U, Niklas KJ: **Macroevolution via secondary endosymbiosis: a Neo-Goldschmidtian view of unicellular hopeful monsters and Darwin's primordial intermediate form.** *Theory Biosci* 2008, **127**:277-289.
40. Cavalier-Smith T: **Membrane heredity and early chloroplast evolution.** *Trends Plant Sci* 2000, **5**:174-182.
41. Cavalier-Smith T: **Deep phylogeny, ancestral groups, and the four ages of life.** *Philos Trans R Soc Lond B: Biol Sci* 2010, **365**:111-132.
42. Cavalier-Smith T: **Origin of the cell nucleus, mitosis and sex: roles of intracellular coevolution.** *Biol Direct* 2010, **5**:7.
43. Cavalier-Smith T: **Rooting the tree of life by transition analysis.** *Biol Direct* 2006, **1**:19.
44. Koonin EV: **On the origin of cells and viruses. Primordial virus world scenario.** *Ann NY Acad Sci* 2009, **1178**:47-64.
45. Koonin EV: **The origin and early evolution of eukaryotes in the light of phylogenomics.** *Genome Biol* 2010, **11**:209.
46. Koonin EV, Wolf YI: **The fundamental units, processes and patterns of evolution, and the Tree of Life conundrum.** *Biol Direct* 2009, **4**:33.
47. Yutin N, Wolf MY, Wolf YI, Koonin EV: **The origins of phagocytosis and eukaryogenesis.** *Biol Direct* 2009, **4**:9.
48. Bowman JL, Floyd SK, Sakakibara K: **Green genes - comparative genomics of the green branch of life.** *Cell* 2007, **129**:229-234.
49. Knoll AH: **Life on a Young Planet.** *The First Three Billion Years of Evolution on Earth* Princeton and Oxford, Princeton University Press; 2003.
50. Gross J, Bhattacharya D: **Uniting sex and eukaryote origins in an emerging oxygenic world.** *Biol Direct* 2010, **5**:53.
51. Davidov Y, Jurekvitch E: **Predation between prokaryotes and the origin of eukaryotes.** *BioEssays* 2009, **31**:748-757.
52. Lane CE, Archibald JM: **The eukaryotic tree of life: Endosymbiosis takes its TOL.** *Trends Ecol Evol* 2008, **23**:268-275.
53. Lane N, Martin W: **The energetics of genome complexity.** *Nature* 2010, **467**:929-934.
54. Kutschera U, Niklas KJ: **The modern theory of biological evolution: an expanded synthesis.** *Naturwissenschaften* 2004, **91**:255-276.
55. Bell G: *Selection: the mechanism of evolution* New York: Chapman and Hall; 1997.
56. Doolittle WF, Bapteste E: **Pattern pluralism and the tree of life hypothesis.** *Proc Natl Acad Sci USA* 2007, **104**:2043-2049.
57. Maxwell JC: **Dynamic Earth.** *J Appl Physics* 1971, **42**:1467.
58. Snider-Pellegrini A: *La Création et ses mystères dévoilés* Franck et Dentú, Paris; 1858.
59. Wegener A: *Die Entstehung der Kontinente und Ozeane. 4. Auflage* Braunschweig, F. Vieweg & Sohn; 1929, (1. Auflage 1915).
60. Skinner BJ, Porter SC: *The Dynamic Earth: An Introduction to Physical Geology.* 5 edition. New York: John Wiley & Sons; 2003.
61. Gould SJ: *The structure of evolutionary theory* Cambridge, Massachusetts, Harvard University Press; 2002.
62. Kutschera U: **Symbiogenesis, natural selection, and the dynamic Earth.** *Theory Biosci* 2009, **128**:191-203.
63. Zhang P, Chen YQ, Zhou H, Lin YF, Wang XL, Papenfuss TJ, Wake DB, Qu LH: **Phylogeny, evolution, and biogeography of Asiatic Salamanders (Hynobiidae).** *Proc Natl Acad Sci USA* 2006, **103**:7360-7365.
64. Nield T: *Supercontinent. Ten billion years in the life of our planet* Cambridge, Harvard University Press; 2007.
65. Steinberger B: **Reconstructing earth history in three dimensions.** *Science* 2008, **322**:866-868.

66. Whelan RJ: *The Ecology of Fire* Cambridge, Cambridge University Press; 1995.
67. Kutschera U: **Plant-associated methylobacteria as co-evolved phytosymbionts. A hypothesis.** *Plant Signal Behav* 2007, **2**:74-78.
68. Franklin JR, Mac Mahon JA, Swanson FJ, Sedell JR: **Ecosystem response to the eruption of Mount St. Helens.** *Nat Geogr Res* 1985, **1**:198-216.
69. Steinman AD, Lamberti GA: **Lotic algal communities in the Mt. St. Helens region six years following the eruption.** *J Phycol* 1988, **24**:482-489.
70. Kutschera U: **Darwin's philosophical imperative and the *Furor Theologicus*.** *Evo Edu Outreach* 2009, **2**:688-694.
71. Reif W-E, Junker T, Hoßfeld U: **The synthetic theory evolution: general problems and the German contribution to the synthesis.** *Theory Biosci* 2000, **119**:41-91.
72. Scheiner SM: **Toward a conceptual framework for biology.** *Quart Rev Biol* 2010, **85**:293-318.
73. Niklas KJ: *The Evolutionary Biology of Plants* Chicago: The University of Chicago Press; 1997.
74. Kutschera U: **From Darwinism to evolutionary biology.** *Science* 2008, **321**:1157-1158.
75. Weiner J: *Planet Earth* New York: Bantam Books; 1986.
76. O'Malley MA: **What did Darwin say about microbes, and how did microbiology respond?** *Trends Microbiol* 2009, **17**:341-347.
77. Müller-Wille S: **The dark side of evolution: Caprice, deceit, redundancy.** *Hist Phil Life Sci* 2009, **31**:183-199.
78. Schopf WJ: **Fossil evidence of Archaean life.** *Phil Trans R Soc B* 2006, **361**:869-885.
79. Doolittle WF, Zhaxybayeva O: **On the origin of prokaryotic species.** *Genome Res* 2009, **19**:744-756.
80. Cracraft J, Donoghue MJ: *Assembling the Tree of Life* Oxford: Oxford University Press; 2004.
81. Kutschera U: **Lay aside the ladder of descent.** *Nature* 2011, **471**:37.
82. Herrada EA, Tessone CJ, Klemm K, Eguiluz M, Hernandez-Garcia E, Duarte CM: **Universal scaling in the branching of the tree of life.** *PLoS One* 2008, **3**:e 2757.
83. Eldredge N: **Macroevolutionary dynamics:Species, niches and adaptive peaks.** New York: McGraw - Hill; 1989.
84. Levin HL: *The Earth through Time.* 7 edition. Hoboken, John Wiley; 2003.
85. Gradstein FM, Ogg JG, Smith AG, (eds): *A geologic time scale 2004* Cambridge University Press, Cambridge; 2004.
86. Szathmary E, Maynard Smith J: *The Major Transitions in Evolution* Oxford: Oxford University Press; 1998.